Zootaxa 4052 (2): 215–225
www.mapress.com/zootaxa/
Copyright © 2015 Magnolia Press

Article

ISSN 1175-5326 (print edition)
ZOOTAXA
ISSN 1175-5334 (online edition)

http://dx.doi.org/10.11646/zootaxa.4052.2.5
http://zoobank.org/urn:lsid:zoobank.org:pub:AF7D9D8E-4DE7-43D0-AA7A-10104E95A6E9

Margelopsis gibbesii (McCrady, 1859) (Cnidaria, Hydrozoa): taxonomic review, and conservation of usage by designation of a lectotype

DALE R. CALDER[1,3] & WILLIAM S. JOHNSON[2]

[1]*Department of Natural History, Royal Ontario Museum, 100 Queen's Park, Toronto, Ontario, Canada M5S 2C6.*
E-mail: dalec@rom.on.ca
[2]*Department of Biological Sciences, Goucher College, 1021 Dulaney Valley Road, Towson, Maryland 21204, USA.*
E-mail: bjohnson090@gmail.com
[3]*Corresponding author*

Abstract

The binomen *Nemopsis gibbesii* McCrady, 1859, originally applied to a species of hydromedusa and its supposed hydroid from South Carolina, USA, has been known for more than a century to encompass two species. The medusa stage is conspecific with that of *Nemopsis bachei* L. Agassiz, 1849, while the hydroid stage is referable to the genus *Margelopsis* Hartlaub, 1897. Both that hydroid, and the medusa stage now subjectively linked to it, are commonly assigned to *M. gibbesii*. With no type having ever been designated for McCrady's species, a lectotype is designated to stabilize nomenclature of the species and serve as the standard for application of the name. In the absence of type specimens, an illustration of the hydroid of *N. gibbesii* by McCrady is chosen as lectotype, thereby conserving the name *Margelopsis gibbesii* in its accustomed usage. Hydroids and medusae of the species are re-described from new material, the cnidome of both stages is characterized, and a taxonomic review is given. The hydroid stage is reported for the first time since its original description in the mid-19th century. Medusae of *M. gibbesii* are also seen infrequently, having been reported only six times earlier.

Key words: Anthoathecata, Aplanulata, Hydroidolina, hydroids, hydromedusae, invertebrates, Medusozoa, taxonomy, zoological nomenclature, zoology

Introduction

In a classic paper on Hydrozoa and hydrozoan life cycles, McCrady (1859) described and named several widely familiar families, genera and species of hydroids and hydromedusae from Charleston Harbor, South Carolina, USA. Taxonomic instability currently exists over *Nemopsis gibbesii* McCrady, 1859, one of the species he described. For more than 130 years, the binomen has been known to have originally included the medusa stage of one species and the hydroid of another. The two species are so different that they have been assigned to different genera (*Nemopsis* L. Agassiz, 1849; *Margelopsis* Hartlaub, 1897) and even families (Bougainvilliidae Lütken, 1850; Margelopsidae Mayer, 1910). No name-bearing type has ever been designated to fix a standard of reference for application of the name *N. gibbesii*.

In the interests of nomenclatural stability, a lectotype is officially designated herein to objectively define the taxon. The identity of the species is thereby stabilized in conformity with the taxonomic concept of *Margelopsis gibbesii*, rather than as a synonym of *Nemopsis bachei* L. Agassiz, 1849. Prevailing usage of the name in literature on Hydrozoa is thus upheld. Both hydroid and medusa stages of the species are described from new material in collections at the Royal Ontario Museum.

Systematic account

Phylum Cnidaria Verrill, 1865

Accepted by A. Marques: 22 Oct. 2015; published: 2 Dec. 2015

Licensed under a Creative Commons Attribution License http://creativecommons.org/licenses/by/3.0

Subphylum Medusozoa Petersen, 1979

Class Hydrozoa Owen, 1843

Subclass Hydroidolina Collins, 2000

Order Anthoathecata Cornelius, 1992

Suborder Aplanulata Collins, Winkelman, Hadrys & Schierwater, 2005

Family Margelopsidae Mayer, 1910

Genus *Margelopsis* Hartlaub, 1897

***Margelopsis gibbesii* (McCrady, 1859)**
Figs. 1, 2

not *Nemopsis gibbesii* McCrady, 1859: 160, pl. 10, figs. 1–3 [medusa] [=*Nemopsis bachei* L. Agassiz, 1849].—Bedot, 1925: 295 [binomen *N. gibbesii* encompasses two species].—Stephens & Calder, 1992: 44, fig. 3, in part (reproduction of McCrady's pl. 10, figs. 1–3) [mention of medusa; historical discussion] [=*Nemopsis bachei*].—Sanders & Anderson, 1999: 58 [medusa; historical discussion] [=*Nemopsis bachei*].

Nemopsis gibbesii McCrady, 1859: 162–163, pl. 10, figs. 4–7 [description of hydroid; description of medusae newly liberated from hydroid].—Allman, 1864: 370; 1872: 362 [mention of hydroid; not adult medusa].—Bedot, 1910: 333 [synonymy].—Schuchert, 2006: 361 [taxonomic discussion].

Nemopsis bachei.—L. Agassiz, 1862: 345 [in part; hydroid of *Nemopsis gibbesi* included in synonymy with *N. bachei*] [not *Nemopsis bachei* L. Agassiz, 1849].

not *Nemopsis bachei*.—L. Agassiz, 1862: 345 [in part; medusa of *Nemopsis gibbesi* included in synonymy with *N. bachei*].—A. Agassiz, 1865: 149 [medusa] [*Nemopsis gibbesi* included in synonymy list] [incorrect subsequent spelling].—Haeckel, 1879: 93 [mention of medusa] [*Nemopsis gibbesii* included in synonymy list].—Brooks, 1883: 468 [mention of medusa] [*Nemopsis gibbesii* included in synonymy list].

Nemopsis gibbesi.—Frech, 1897: 565 [mention of hydroid].—Hartlaub, 1899: 221, fig. 4; 1903: 28 [mention of hydroid].—Bedot, 1918: 358 [synonymy: *N. gibbesi* = *Margelopsis gibbesi* in part] [incorrect subsequent spelling].

Margelopsis gibbesii.—Hartlaub, 1899: 224 [mention of hydroid].—Mayer, 1910, pl. 9, figs. 4–7 [illustration of medusa].—Stephens & Calder, 1992: 44, fig. 3, in part (reproduction of McCrady's pl. 10, figs. 4–7) [mention of hydroid & young medusa; historical discussion].—Sanders & Anderson, 1999: 58 [historical discussion].—Cairns *et al*., 2002: 14 [listing of hydroid]; 17 [listing of medusa].—Schuchert, 2006: 361 [taxonomic discussion].—Johnson & Allen, 2012: 94, fig. p. 95 [report of medusa].

Margelopsis gibbesi.—Hartlaub, 1903: 28 [mention of hydroid].—Hartlaub, 1907: 92 [mention of hydroid].—Mayer, 1910: 82 [report of medusa]; 83 [mention of hydroid].—Ritchie, 1915: 563 [mention of hydroid].—Bedot, 1918: 184 [literature].—Bedot, 1925: 279 [literature].—Uchida, 1927: 196 [mention of medusa].—Rees, 1941: 134 [mention of hydroid].—Fraser, 1944: 104, pl. 18, fig. 77; 1946: 156 [description of hydroid and young medusa based on McCrady 1859].—Miner, 1950: 102, figs. pl. 35 [guidebook; mention of hydroid; mention of medusa].—Werner, 1955a: 8 [mention of medusa].—Kramp, 1959: 92, fig. 48 [account of medusa from literature].—Kramp, 1961: 49 [literature: review of medusa stage].—Allwein, 1967: 122 [report of medusa].—Gosner, 1971: 111, fig. 5.18B [guidebook; mention of medusa].—Sandine & Swiecicki, 1975: 83 [technical report; report of medusa].—Hester, 1976: 19, pl. 1, fig. 4 [thesis; report of medusa].—Tatham *et al*., 1977: 141 [technical report; report of medusa].—Calder & Hester, 1978: 88 [mention of hydroid; mention of medusa].—Harrison *et al*., 1979: 37 [mention of hydroid; mention of medusa; species of "special concern"].—Cairns *et al*., 1991: 16 [listing of hydroid]; 20 [listing of medusa].—Bouillon & Boero, 2000: 145 [listing of hydroid; listing of medusa].—Bouillon *et al*., 2006: 245, fig. 118B [listing of hydroid; listing of medusa; figure of medusa, from Kramp 1959 after Mayer 1910] [incorrect subsequent spelling].

not *Margelopsis gibbesi*.—Thiel, 1938: 294 [misidentification of medusa] [=*Margelopsis australis* Browne, 1910].

Margelopsis.—Werner, 1954: 144 [reference to McCrady's 1859 hydroid].

M. (as *Margelipsis*) *gibbsi*.—Zamponi, 1983: 178 [mention of medusa] [incorrect subsequent spelling].

Type Locality. USA: Charleston Harbor, South Carolina (McCrady 1859).

Material examined. Virginia Beach, Virginia, from aquaria operated by Hampton Roads Sanitation District, May 1989, 22‰, several dozen hydroids, some with medusa buds, coll. Ms. Butterworth, ROMIZ B1027.—Chincoteague, Virginia, Station 199, about 5 km offshore, depth 10 m, 24.iv.2006, epibenthic sled, <20 cm off bottom, two male medusae, coll. W. Johnson, ROMIZ B4077.—Assateague Island, Virginia, Station 208, just off beach near southern tip of island, surf zone, depth 1–2 m, 10.vi.2006, epibenthic sled, <20 cm off bottom, three female medusae, some with nascent polyps, coll. W. Johnson, ROMIZ B4078.—Assateague Island, Virginia, Station 221, ca. 200 m off beach near southern tip of island, depth 5 m, 10.vi.2006, epibenthic sled, <20 cm off bottom, one male medusa, coll. W. Johnson, ROMIZ B4079.—Assateague Island, Virginia, ca. 400 m offshore, depth 5 m, 10.vi.2006, epibenthic sled, <20 cm off bottom, about 35 female medusae, some with nascent polyps, and four male medusae, coll. W. Johnson, ROMIZ B4080.

Description of material. Hydroids solitary, naked, monomorphic, free-floating. Hydranths all young, minute (< 1 mm long), typically vasiform to pear-shaped, with dome-shaped hypostome at distal end and vestigial hydrocaulus at proximal end; mouth at tip of hypostome. Hydrocaulus with base hollowed out, having a sucker-like appearance. Tentacles appearing moniliform, in widely separated oral and aboral whorls; oral tentacles 5–7 in number; aboral tentacles 7–9 in number, slightly larger than oral ones. Some hydranths appearing to undergo asexual reproduction by transverse fission (Fig. 1e) and budding (Fig. 1f).

Gonophores medusa buds arising on hydranth distal to aboral tentacular whorl; all observed medusa buds very early in development.

Medusae thimble-shaped with rounded apex, up to 2.3 mm high, 1.9 mm wide; mesoglea of moderate thickness. Exumbrellar surface with scattered nematocysts, possibly subspherical heteronemes, and nematocyst patches. Apical canal present, narrow, inconspicuous. Manubrium vasiform, extending nearly to velar opening, proximal end with vacuolated gastrodermal cells. Mouth irregularly circular, without lips or oral tentacles. Radial canals four, simple. Ring canal present. Marginal bulbs four, pyriform. Ocelli lacking. Marginal tentacles 5–8 per marginal bulb, moniliform, with nematocysts arranged in rings and with an elongated terminal bulb. Velum well-developed. Gonad surrounding manubrium except at upper and lower extremities. Female medusae with prominent subitaneous eggs extruded from gonad, some developing as nascent polyps (actinulae). Developing polyps subspherical to discoidal at release, about 0.3 mm in diameter, with approximately 12–13 short tentacles

.

Cnidome of hydroid.

Desmonemes (n = 10): 5.0–5.8 µm long × 2.6–3.3 µm wide (undischarged)
Haplonemes (n = 10): 6.3–7.4 µm long × 2.5–3.6 µm wide (undischarged)
Microbasic heteronemes (n = 10): 7.0–8.4 µm long × 2.8–3.6 µm wide (undischarged)

Cnidome of medusa.

Desmonemes (n = 10): 3.7–4.0 µm long × 2.8–3.2 µm wide (undischarged)
Haplonemes (n = 5): 5.0–6.4 µm long × 1.6–2.5 µm wide (undischarged)
Microbasic heteronemes (n = 10): 5.0–6.1 µm long × 2.8–3.6 µm wide (undischarged)
Subspherical heteronemes (n = 10): 8.4–9.5 µm long × 7.5–8.6 µm wide (undischarged)
Stenoteles (n = 10): 5.8–7.3 µm long × 4.0–5.9 µm wide (undischarged)

Historical account. Under the name *Nemopsis gibbesii*, McCrady (1859) described and illustrated a medusa from Charleston Harbor, South Carolina, that he regarded as a new species. Included with it was an account of a hydroid, also illustrated, that he took to be its polyp stage. McCrady recognized that the medusa was referable to the same genus as *Nemopsis bachei* L. Agassiz, 1849 from New England, but considered it to be specifically distinct. The hydroid he associated with the species bore medusa buds, and medusae were liberated from it. Apparently seen only once by him, it was found during January as a free-floating, solitary polyp having a rudimentary hydrocaulus and two whorls of tentacles. Medusae attributed to *N. gibbesii* were observed during winter and spring.

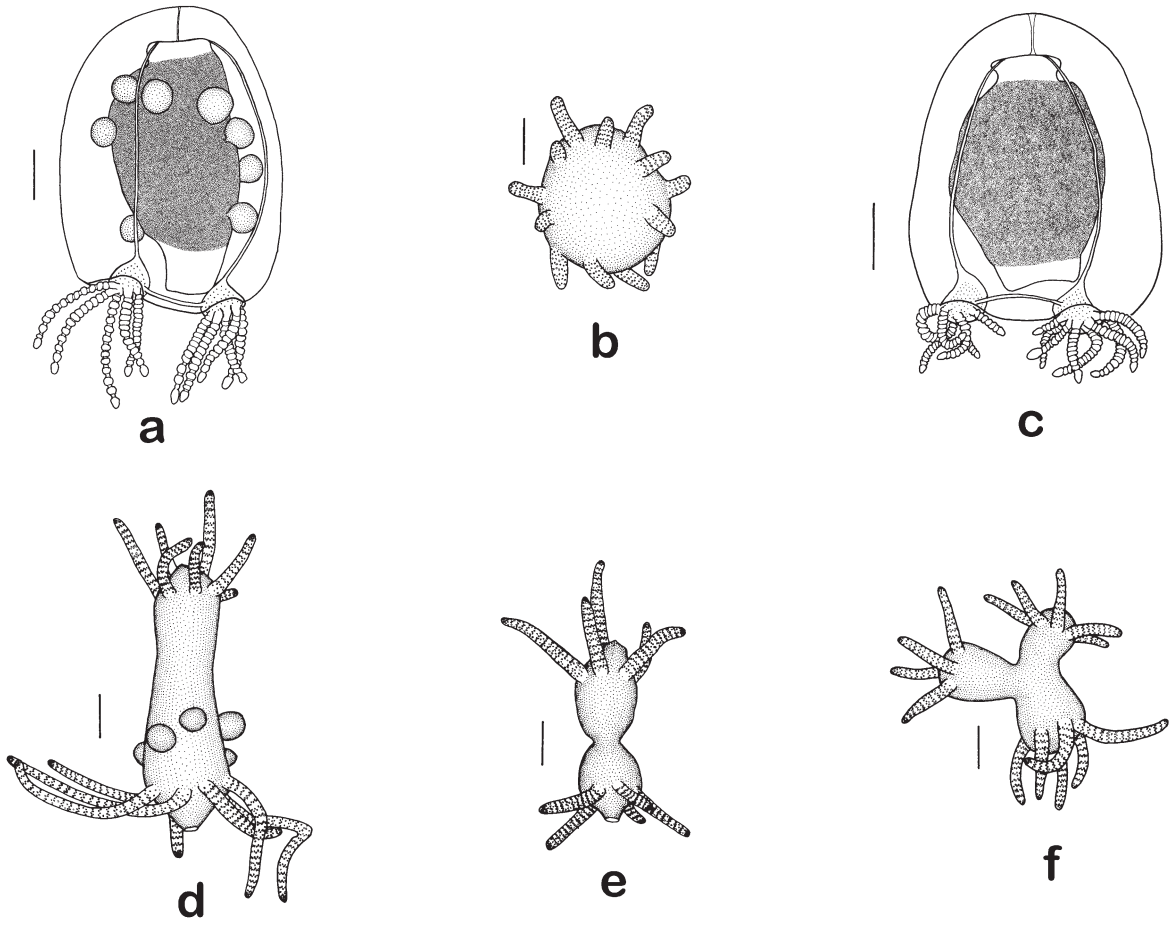

FIGURE 1. *Margelopsis gibbesii*, hydroid and medusa stages from preserved samples. **a**, mature female medusa with subitaneous eggs, ROMIZ B4078. **b**, larval polyp released from gonad of female medusa, ROMIZ B4078. **c**, mature male medusa, ROMIZ B4077. **d**, hydroid with medusa buds, ROMIZ B1027. **e**, small hydroid appearing to undergo fission, ROMIZ B1027. **f**, small hydroid appearing to undergo budding, ROMIZ B1027. Scale bars: a = 0.25 mm; b, d–f = 0.1 mm; c = 0.5 mm.

Without comment, but surely based on the medusa stage only, L. Agassiz (1862: 345) included *Nemopsis gibbesii* (spelled therein as *N. gibbesi*) in the synonymy of *N. bachei*. Following studies on the medusa stage of *N. bachei* in New England, A. Agassiz (1865) also included *N. gibbesii* (again spelled *N. gibbesi*) as a subjective synonym. The only reservation he expressed in doing so was based on seasonality of populations at the two locations, with those from Charleston occurring in winter and those from Vineyard Sound being common in September. After searching for the hydroid stage without success, the younger Agassiz concluded that McCrady's planktonic polyp had simply been a detached hydranth of a benthic species.

Brooks (1883) was first to unequivocally establish that the hydroid and medusa stages attributed to *Nemopsis gibbesii* by McCrady (1859) were different species. He raised medusae identical to the original account of *N. gibbesii* from a benthic colonial hydroid reportedly resembling species of *Eudendrium* Ehrenberg, 1834 or *Bougainvillia* Lesson, 1830, both morphologically quite unlike the polyp described by McCrady. His observations on development of the species supported the hypothesis that medusae of *N. gibbesii* and *N. bachei* were conspecific. However, that confirmation did not fully resolve the taxonomic identity of the nominal species *N. gibbesii*. No type specimen had been designated to objectively define it, whether hydroid or medusa, and the true affinities of McCrady's remarkable hydroid remained unknown. As with A. Agassiz (1865) earlier, Allman (1872) questioned whether the trophosome was indeed a normally free-floating polyp.

The generic identity of the hydroid McCrady (1859) had assigned to *Nemopsis gibbesii* was finally resolved by

Hartlaub (1899) through life cycle studies of the European medusa *Margelopsis haeckelii* Hartlaub, 1897. He discovered that its hydroid stage was a solitary, planktonic polyp much like that described by McCrady. Hartlaub thereupon assigned McCrady's hydroid to *Margelopsis* Hartlaub, 1897, as *M. gibbesii*. The medusa stage of the American hydroid remained unknown until Mayer (1910) discovered and described specimens from North Carolina and South Carolina, referring to them as *Margelopsis gibbesi* in the text (p. 82) and as *M. gibbesii* in captions accompanying Plate 9. While the link between McCrady's hydroid and Mayer's medusa is subjective, not having been based on a complete life cycle study, it seems probable that they are conspecific. For more than a century, the name *M. gibbesi* has commonly been applied to the two stages (see synonymy list above). Both hydroid and medusa appear endemic to the southeast and mid-Atlantic coasts of the United States. A report of the species from the South Atlantic Ocean between South Georgia and Bouvet Island by Thiel (1938) is believed to have been based instead on *M. australis* Browne, 1910 (Kramp 1961: 49).

Nomenclature and taxonomy. As apparent from the synonymy list above, the specific name of McCrady's species has been spelled in the literature as both *gibbesii* and *gibbesi*. Following provisions of the *International Code of Zoological Nomenclature* (ICZN) (International Commission on Zoological Nomenclature 1999), *gibbesii* is the original and correct spelling (ICZN Art. 32). The name honours noted South Carolina mathematician and naturalist Lewis Reeve Gibbes (1810–1894) (Sanders & Anderson 1999; Stephens 2000).

Although the identities of the hydroid and medusa described by McCrady (1859) have long been known, nomenclatural uncertainty persists over the concept of the species to which they were assigned. The taxonomic identity of *Nemopsis gibbesii* remains ambiguous because of the absence of a name-bearing type for a binomen that originally included two species. McCrady did not designate a holotype of *N. gibbesii*, and no syntype specimens are known to exist. His collections, including types, are thought to have been destroyed by fire during the American Civil War (Stephens & Calder 1992: 44). We are also unaware of any previous lectotype or neotype selections.

To stabilize the taxonomic identity of *Nemopsis gibbesii*, we select as lectotype the hydroid specimen illustrated by McCrady (1859) in Plate 10, Figure 7 following ICZN Arts. 74.7.1, 74.7.2, and 74.7.3. Our designation is not invalidated by "…the fact that the specimen no longer exists or cannot be traced" (ICZN Article 74.4). The lectotype chosen here upholds prevailing usage of the name *Margelopsis gibbesii* for both hydroid and medusa stages of the species since the turn of the 20th century. Had one of the medusae illustrated in McCrady's work (Plate 10, Figures 1–3) been chosen as lectotype, *N. gibbesii* would become a subjective synonym of *N. bachei*. A new specific name for the species widely known as *M. gibbesii* would then be required, an act we consider unnecessary and undesirable.

Margelopsidae, the name of the family to which *M. gibbesii* belongs, is sometimes credited in error to Uchida (1927). Under the Principle of Coordination in nomenclature (ICZN Art. 36), authorship and date should be credited instead to Mayer (1910). Although Mayer established the name as Margelopsinae, for a subfamily, he is deemed under that article of the code to have simultaneously established coordinate names for all other ranks of the family group, including the name Margelopsidae.

Two other genera, *Pelagohydra* Dendy, 1902 and *Climacocodon* Uchida, 1924, are usually included with *Margelopsis* in the family Margelopsidae (e.g. Uchida 1924; Kramp 1961; Petersen 1990; Bouillon *et al*. 2006; Schuchert 2006). When *Pelagohydra* and *Margelopsis* are included in the same family, a nomenclatural issue arises because the infrequently used family name Pelagohydridae Dendy, 1902 predates the more familiar name Margelopsidae Mayer, 1910. The two had earlier been recognized as distinct subfamilies by Rees (1941), with Margelopsinae (including *Margelopsis* and *Climacocodon*) having whorls of tentacles on the hydranth and lacking a float, and Pelagohydrinae (including only *Pelagohydra*) having scattered tentacles over the entire hydranth and having the proximal portion of the hydranth modified into a float. Unfortunately, the adult medusa stage of *Pelagohydra* is as yet unknown for comparison with that of *Margelopsis*. Following Schuchert (2006: 356), prevailing usage of the name Margelopsidae is maintained here pending a taxonomic or nomenclatural resolution of the problem.

The family Margelopsidae has generally been classified within the superfamily Tubularioidea Fleming, 1828 (e.g. Rees 1957; Bouillon 1985; Petersen 1990). The latter group has recently been transferred from the suborder Capitata Kühn, 1913 to Aplanulata Collins, Winkelman, Hadrys & Schierwater, 2005 (Cartwright & Nawrocki 2010; Nawrocki *et al*. 2013). Molecular evidence supporting inclusion of Margelopsidae in Aplanulata, however, is still lacking (Peter Schuchert, personal communication, 30 June 2015). The six species commonly included in the

family (*Margelopsis gibbesii*, *M. haeckelii*, *M. hartlaubii*, *M. australis*, *Pelagohydra mirabilis*, and *Climacocodon ikarii*) all appear to be of infrequent occurrence, and specimens have been difficult to obtain for analysis. As for the name Tubularioidea, authorship of it should be credited to Fleming (1828). While the name "Tubulariae" had been used earlier in both Goldfuss (1818) and Fischer von Waldheim (1823), it was not rendered available in either of those works (ICZN Art. 11.7.1.1). As used in them, "Tubulariae" was merely a descriptive term applied to groups that excluded the genus *Tubularia* Linnaeus, 1758 (see Calder 2010: 45).

Purported morphological differences between *M. gibbesii* from the western North Atlantic and *M. haeckelii* from the eastern North Atlantic need re-examination. In a key to medusa stages of species of *Margelopsis*, Kramp (1959) highlighted three characters based on then-existing descriptions that seemed to discriminate the two. *Margelopsis haeckelii* was distinguished by having 3–4 tentacles on each marginal bulb, a wide axial canal above the manubrium in adults, and eggs that developed into actinula-like larval stages on the manubrium. In *M. gibbesii*, 5–6 tentacles were said to arise from each marginal bulb, no wide axial canal was known to exist above the manubrium in adults, and no actinula-like larval stages were thought to occur on the manubrium. The latter distinction has been shown here to be inaccurate; some female medusae of *M. gibbesii* studied by us were observed with developing larval polyps just as in *M. haeckelii*. Meanwhile, the other two characters require further evaluation. Several medusae of *M. gibbesii* in our material possessed an axial canal, although it was narrow in each case. As for numbers of marginal tentacles, Werner (1955a) reported as many as 8–9 on one or more of the marginal bulbs of *M. haeckelii*. Up to eight were seen on the bulbs of a large male of *M. gibbesii* examined during this study (ROMIZ B4077). The hydroid stage of *M. gibbesii* is still too poorly known to reliably assess how it may differ, if at all, from that of *M. haeckelii*. Overall, it seems best to maintain the two as distinct species for now, an opinion expressed earlier by Schuchert (2006).

Live medusae of *M. gibbesii* were examined and described by Mayer (1910). The umbrella was said to be highly contractile. When relaxed, the manubrium reached little more than half-way along the length of the subumbrellar cavity but when contacted, the mouth often extended beyond the velar opening. The endoderm of the marginal bulbs was dull-yellow in colour, while that of the manubrium varied from dull-yellow to dull-green. In *M. haeckelii*, marginal bulbs are brown while the manubrium is gray with dark-brown pigment granules (Schuchert 2006).

Life cycle. The life cycle of *Margelopsis gibbesii* has yet to be adequately described. Werner (1954, 1955a, b, 1956) traced the remarkable life cycle of *M. haeckelii*, and it seems likely that *M. gibbesii* follows a similar pattern inasmuch as hydroids of both species are predominantly planktonic. Notably too, female medusae of both species extrude subitaneous eggs that develop into nascent polyps before being released into the water. Present also in *M. haeckelii* are resting eggs that settle on bottom and become encysted as a dormant stage. Existence of such eggs in *M. gibbesii* seems likely but has yet to be confirmed. Meanwhile, male medusae are said to be extremely rare in *M. haeckelii*, and development is thought to be largely parthenogenetic (Werner 1954, 1955a, 1956; Schuchert 2006). By contrast, males appear to be at least occasional in populations of *M. gibbesii* (Mayer 1910; this study).

Hydroids of *Margelopsis gibbesii* examined here were received for identification in 1989 from the Hampton Roads Sanitation District, Virginia Beach, Virginia (ROMIZ B1027). Discovered in aquaria, they were described as a pest by the collector and donor of the material (Ms. Butterworth, personal communication, May 1989). Remains of brine shrimp, their likely prey in the tanks, were observed together with the hydroid specimens. Hydrozoans are a frequent problem in closed system culture tanks and aquaria. Successful as competitors for food, flourishing under favourable environmental conditions, and lacking predators, populations may rapidly increase in abundance. Some stages may also prey directly on organisms under culture, such as larval decapod crustaceans (Sandifer *et al*. 1974). Resistant or resting stages, known to occur in many hydrozoans (Calder 1990) including *M. haeckelii* (Werner 1954, 1955a, b) and the related *Climacocodon ikarii* Uchida, 1924 (Kubota 1993), make them especially persistent. Meanwhile, *M. gibbesii* was considered a species of "special concern" by Harrison *et al*. (1979) in South Carolina because of its restricted distribution, infrequent occurrence, and the seeming vulnerability of the hydroid stage.

Remarkably, this is the first record of the hydroid of *M. gibbesii* since it was first described and illustrated by McCrady (1859). While small and easily overlooked, it might also be readily dismissed during examination of plankton samples as an insignificant and unidentifiable detached hydranth. The medusa stage is also rarely seen, having been reported only six times earlier (Mayer 1910; Allwein 1967; Sandine & Swiecicki 1975; Hester 1976; Tatham *et al*. 1977; Johnson & Allen 2012).

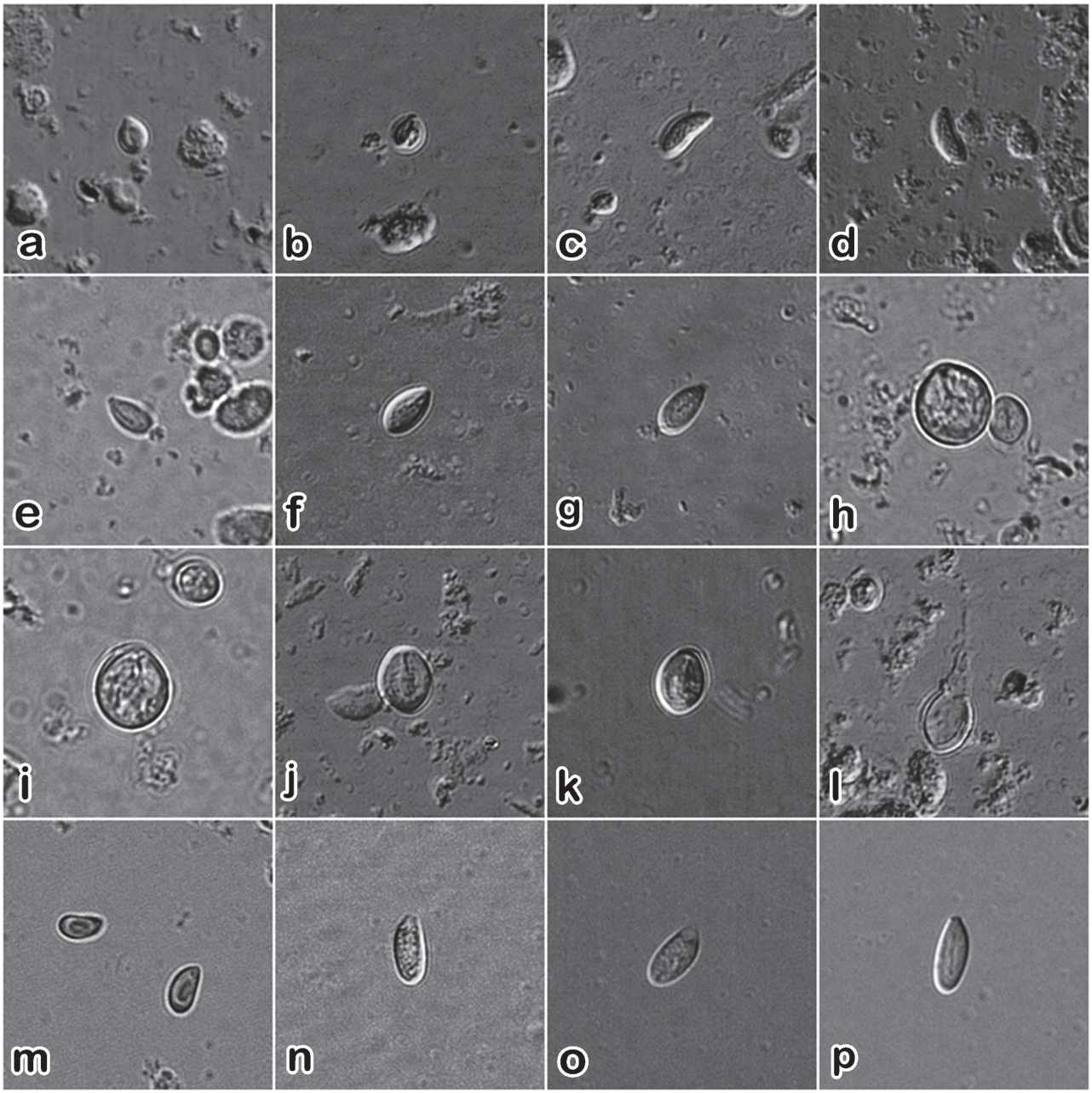

FIGURE 2. Nematocysts of *Margelopsis gibbesii*. Medusa: **a**, desmoneme, from tentacle; **b**, desmoneme, from tentacle; **c**, haploneme, from tentacle; **d**, haploneme, from manubrium; **e**, microbasic heteroneme, from tentacle; **f**, microbasic heteroneme, from tentacle; **g**, microbasic heteroneme, from manubrium; **h**, subspherical heteroneme, from tentacle; **i**, subspherical heteroneme, from tentacle; **j**, stenotele, from tentacle; **k**, stenotele, from tentacle; **l**, discharged stenotele, from tentacle. Hydroid: **m**, desmoneme; **n**, haploneme; **o**, haploneme; **p**, heteroneme. For nematocyst sizes, see text.

Cnidome. Studies were undertaken to document the cnidome of *M. gibbesii*. With few discharged capsules being found in preserved specimens, and with all observed nematocysts being small, their identification was problematic. Categories observed in medusae of the species included desmonemes (Figs. 2a, b), haplonemes (Figs. 2c, d), microbasic heteronemes (Figs. 2e–g), subspherical heteronemes (Figs. 2h, i), and stenoteles (Figs. 2j–l). Of all these types, stenoteles were by far the most abundant. It could not be determined with certainty whether microbasic heteronemes were euryteles or mastigophores. The nematocyst complement of the hydroid stage of *M. gibbesii* was conspicuously different from that of the medusa, most notably in the absence of stenoteles. Categories present included desmonemes (Fig. 2m), haplonemes (Figs. 2n, o), and microbasic heteronemes (Fig. 2p), with desmonemes and microbasic heteronemes being most abundant. Again, heteronemes may have been either mastigophores or euryteles. By comparison, Schuchert (2006) reported desmonemes, microbasic mastigophores

and stenoteles in medusae of *Margelopsis hartlaubii* Browne, 1903, with stenoteles apparently occurring only around the mouth opening. According to Bouillon (1974: 37), the nematocyst complement in hydroids of *M. haeckelii* comprises desmonemes, basitrichs, microbasic euryteles, and stenoteles. Nematocysts of the closely related *Climacocodon ikarii* from Japan were identified as large and small stenoteles and microbasic euryteles in both medusa and hydroid stages (Kubota 1976, 1979). Curiously, no desmonemes were found. Finally, the cnidome of *Pelagohydra mirabilis* Dendy, 1902, a margelopsid from New Zealand, comprised stenoteles and desmonemes in the hydroid, while that of the young medusa comprised stenoteles, desmonemes, heteronemes, and haplonemes (Schuchert, 1996). The apparent absence of stenoteles in our hydroids of *M. gibbesii* was unexpected inasmuch as these nematocysts are almost universally present in capitate and aplanulate hydrozoans.

Seasonality. *Margelopsis gibbesii* has been reported during colder months of the year along its known range (January, Charleston, South Carolina, hydroid, McCrady 1859; November, Oregon Inlet and Southport, North Carolina, medusa, Mayer 1910; December, Beaufort, South Carolina, medusa, Mayer 1910; March and April, Beaufort, North Carolina, medusa, Allwein 1967; winter-spring, off Little Egg Inlet, New Jersey, Sandine & Swiecicki 1975; December, 17.2° C, 32.19‰, Deveaux Bank, South Carolina, medusa, Hester 1976; February and March, Barnegat Bay, New Jersey, medusa, Tatham *et al.* 1977; April and June, eastern shore of Virginia, medusa, this study). The species tolerates brackish conditions (Mayer 1910), and polyps examined here had been thriving in aquaria at 22‰.

Reported distribution. Charleston Harbor, South Carolina: planktonic hydroid (McCrady 1859: 163, as *Nemopsis gibbesii*).–Oregon Inlet, North Carolina: medusa; Southport, North Carolina: medusa; Beaufort, South Carolina: medusa (Mayer 1910: 82, as *Margelopsis gibbesi* in text; as *M. gibbesii* in figure captions).–Beaufort, North Carolina: medusa (Allwein 1967: 122, *as M. gibbesi*).–Off Little Egg Inlet, New Jersey: medusa (Sandine & Swiecicki 1975: 129, 146).–Deveaux Bank, South Carolina: medusa (Hester 1976: 60, *as M. gibbesi*).–Barnegat Bay, New Jersey: medusa (Tatham *et al.* 1977: 141, 143, 331, as *M. gibbesi*).–Maryland to South Carolina: medusa (Johnson & Allen 2012: 94).–Virginia Beach, Virginia: hydroid in aquaria; off Chincoteague, Virginia, and Assateague Island, Virginia: medusa (reported herein).

Acknowledgements

Sincere thanks are extended to Dr. A.C. Marques, Centro de Biologia Marinha (CEBIMar), Universidade de São Paulo, for editorial assistance. Three anonymous referees are acknowledged for helpful reviews. We are grateful to Dr. Peter Schuchert, Muséum d'Histoire Naturelle (MHN), Geneva, Switzerland, for offering constructive comments on an early draft of this manuscript. Thanks are also due to Maureen Zubowski of the Royal Ontario Museum for collections management assistance, and to Lynn Barrett of the University of Toronto for bibliographic help.

References

Agassiz, A. (1865) *Illustrated catalogue of the Museum of Comparative Zoölogy, at Harvard College. No. II. North American Acalephae*. Sever & Francis, Cambridge, Massachusetts, 234 pp.

Agassiz, L. (1849) Contributions to the natural history of the Acalephae of North America. Part I.–On the naked-eyed medusae of the shores of Massachusetts, in their perfect state of development. *Memoirs of the American Academy of Arts and Sciences*, 4, 221–316.
http://dx.doi.org/10.2307/25058163

Agassiz, L. (1862) *Contributions to the natural history of the United States of America. Vol. IV.* Little, Brown & Company, Boston, 380 pp.

Allman, G.J. (1864) On the construction and limitation of genera among the Hydroida. *Annals and Magazine of Natural History*, Series 3, 13, 345–380.

Allman, G.J. (1872) A monograph of the gymnoblastic or tubularian hydroids. Conclusion of Part I, and Part II, containing descriptions of the genera and species of the Gymnoblastea. Vol. II. *Ray Society Publication*, 47, 155–450.

Allwein, J. (1967) North American hydromedusae from Beaufort, North Carolina. *Videnskabelige Meddelelser fra Dansk Naturhistorisk Forening*, 130, 117–136.

Bedot, M. (1910) Matériaux pour servir à l'histoire des hydroïdes. 3^{me} période (1851 à 1871). *Revue Suisse de Zoologie*, 18, 189–490.

http://dx.doi.org/10.5962/bhl.part.75203
Bedot, M. (1918) Matériaux pour servir à l'histoire des hydroïdes. 6e période (1891 à 1900). *Revue Suisse de Zoologie* 26 (Fascicule Supplémentaire), 1–376.
Bedot, M. (1925) Matériaux pour servir à l'histoire des hydroïdes. 7e période (1901 à 1910). *Revue Suisse de Zoologie*, 32 (Fascicule Supplémentaire), 1–657.
Bouillon, J. (1974) Sur la structure de *Paracoryne huvei*, Picard 1957 (Coelenterata, Hydrozoa, Athecata). *Académie Royale de Belgique, Mémoires de la Classe des Sciences,* Collection in-4°, Série 2e, 18 (3), 5–45.
Bouillon, J. (1985) Essai de classification des hydropolypes–hydroméduses (Hydrozoa–Cnidaria). *Indo-Malayan Zoology*, 1 (1985), 29–243.
Bouillon, J. & Boero, F. (2000) Phylogeny and classification of Hydroidomedusae. *Thalassia Salentina*, 24, 1–296.
Bouillon, J., Gravili, C., Pagès, F., Gili, J.-M. & Boero, F. (2006) An introduction to Hydrozoa. *Mémoires du Muséum National d'Histoire Naturelle*, 194, 1–591.
Brooks, W.K. (1883) Notes on the medusae of Beaufort, N.C. Part II. *Studies from the Biological Laboratory, Johns Hopkins University*, 2, 465–475.
Browne, E.T. (1903) Report on some medusae from Norway and Spitzbergen. *Bergens Museums Aarbog*, 4, 1–36.
Browne, E.T. (1910) Coelentera. V.–Medusae. *National Antarctic Expedition 1901–1904. Natural History, Zoology and Botany*, (5), 1–62.
Cairns, S.D., Calder, D.R., Brinckmann-Voss, A., Castro, C.B., Pugh, P.R., Cutress, C.E., Jaap, W.C., Fautin, D.G., Larson, R.J., Harbison, G.R., Arai, M.N. & Opresko, D.M. (1991) Common and scientific names of aquatic invertebrates from the United States and Canada: Cnidaria and Ctenophora. *American Fisheries Society Special Publication*, 22, 1–75.
Cairns, S.D., Calder, D.R., Brinckmann-Voss, A., Castro, C.B., Fautin, D.G., Pugh, P.R., Mills, C.E., Jaap, W.C., Arai, M.N., Haddock, S.H.D. & Opresko, D.M. (2002) Common and scientific names of aquatic invertebrates from the United States and Canada: Cnidaria and Ctenophora. 2nd Edition. *American Fisheries Society Special Publication*, 28, 1–115.
Calder, D.R. (1990) Seasonal cycles of activity and inactivity in some hydroids from Virginia and South Carolina, USA. *Canadian Journal of Zoology*, 68, 442–450.
http://dx.doi.org/10.1139/z90-065
Calder, D.R. (2010) Some anthoathecate hydroids and limnopolyps (Cnidaria, Hydrozoa) from the Hawaiian archipelago. *Zootaxa*, 2590, 1–91.
Calder, D.R. & Hester, B.S. (1978) Phylum Cnidaria. *In*: Zingmark, R.G. (Ed.), *An annotated checklist of the biota of the coastal zone of South Carolina*. University of South Carolina Press, Columbia, pp. 87–93.
Cartwright, P. & Nawrocki, A.M. (2010) Character evolution in Hydrozoa (phylum Cnidaria). *Integrative and Comparative Biology*, 50, 456–472.
http://dx.doi.org/10.1093/icb/icq089
Collins, A.G. (2000) Towards understanding the phylogenetic history of Hydrozoa: hypothesis testing with 18S gene sequence data. *Scientia Marina*, 64 (Suplemento 1), 5–22.
http://dx.doi.org/10.3989/scimar.2000.64s15
Collins, A.G., Winkelmann, S., Hadrys, H. & Schierwater, B. (2005) Phylogeny of Capitata and Corynidae (Cnidaria, Hydrozoa) in light of mitochondrial 16S rDNA data. *Zoologica Scripta*, 34, 91–99.
http://dx.doi.org/10.1111/j.1463-6409.2005.00172.x
Cornelius, P.F.S. (1992) Medusa loss in leptolid Hydrozoa (Cnidaria), hydroid rafting, and abbreviated life-cycles among their remote-island faunae: an interim review. *Scientia Marina*, 56, 245–261.
Dendy, A. (1902) On a free-swimming hydroid, *Pelagohydra mirabilis*, n. gen. et sp. *Quarterly Journal of Microscopical Science*, New Series, 46, 1–24.
Ehrenberg, C.G. (1834) Beiträge zur physiologischen Kenntniss der Corallenthiere im allgemeinen, und besonders des rothen Meeres, nebst einem Versuche zur physiologischen Systematik derselben. *Abhandlung der Königlichen Akademie der Wissenschaften, Berlin*, 1, 225–380.
Fischer von Waldheim, G. (1823) *Enchiridion generum animalium*. Publisher not identified, Moscow, 32 pp.
http://dx.doi.org/10.5962/bhl.title.42223
Fleming, J. (1828) *A history of British animals, exhibiting the descriptive characters and systematical arrangement of the genera and species of quadrupeds, birds, reptiles, fishes, Mollusca, and Radiata of the United Kingdom*. Bell & Bradfute, Edinburgh, 565 pp.
http://dx.doi.org/10.5962/bhl.title.12859
Fraser, C.M. (1944) *Hydroids of the Atlantic coast of North America*. University of Toronto Press, Toronto, 451 pp.
Fraser, C.M. (1946) *Distribution and relationship in American hydroids*. University of Toronto Press, Toronto, 464 pp.
Frech, F. (1897) *Lethaea geognostica oder Beschreibung und Abbildung der für die Gebirgs–Formationen bezeichnendsten Versteinerungen. Herausgegeben von einer Vereinigung von Palaeontologen. II. Graptolithiden. 1. Theil. Lethaea palaeozoica. 1. Band*. E. Schweizerbart'sche Verlagshandlung, Stuttgart, 142 pp. [pp. 544–684]
Goldfuss, G.A. (1818) Ueber die Classification der Zoophyten. *Isis oder Encyclopädische Zeitung von Oken*, 1818, 1008–1013.
Gosner, K.L. (1971) *Guide to identification of marine and estuarine invertebrates. Cape Hatteras to the Bay of Fundy.* Wiley-Interscience, New York, 693 pp.
Haeckel, E. (1879) Das System der Medusen. Erster Theil einer Monographie der Medusen. *Denkschriften der Medicinisch-*

Naturwissenschaftlichen Gesellschaft zu Jena, 1, 1–360.
Harrison, F.W., Calder, D.R., Coull, B.C. & James, F.C. (1979) Status report: lower invertebrates and miscellaneous phyla. *In*: Forsythe, D.M. & Ezell, W.B. (Eds.), *Proceedings of the First South Carolina Endangered Species Symposium, Charleston, South Carolina*, pp. 34–40.
Hartlaub, C. (1897) Die Hydromedusen Helgolands. Zweiter Bericht. *Wissenschaftliche Meeresuntersuchungen*, Neue Folge, 2, 449–537.
Hartlaub, C. (1899) Zur Kenntniß der Gattungen *Margelopsis* und *Nemopsis*. *Nachrichten von der Königlichen Gesellschaft der Wissenschaften zu Göttingen, Mathematisch–Physikalische Klasse*, 1899, 219–224.
Hartlaub, C. (1903) Coelenterata. Dendy, A., On a free-swimming hydroid, *Pelagohydra mirabilis* n. gen. n. sp. *In:* Quart. Journ. microsc. Sc. Vol. 46. N.S. 1902. Page. 1–24. Pls. 1–2. *Zoologisches Zentralblatt*, 10, pp. 27–34.
Hartlaub, C. (1907) XII. Craspedote Medusen. I. Teil. 1. Lief.: Codoniden und Cladonemiden. *Nordisches Plankton*, 6, 1–135.
Hester, B.S. (1976) *Distribution and seasonality of hydromedusae in South Carolina estuaries*. M.S. Thesis, College of Charleston, Charleston, South Carolina, 88 pp.
International Commission on Zoological Nomenclature (1999) *International code of zoological nomenclature. 4th Edition*. International Trust for Zoological Nomenclature, London, 306 pp.
Johnson, W.S. & Allen, D.M. (2012) *Zooplankton of the Atlantic and Gulf coasts. A guide to their identification and ecology. 2nd Edition.* Johns Hopkins University Press, Baltimore, 452 pp.
Kramp, P.L. (1959) The hydromedusae of the Atlantic Ocean and adjacent waters. *Dana-Report*, 46, 1–283.
Kramp, P.L. (1961) Synopsis of the medusae of the world. *Journal of the Marine Biological Association of the United Kingdom*, 40, 1–469.
http://dx.doi.org/10.1017/s0025315400007347
Kubota, S. (1976) Notes on the nematocysts of Japanese hydroids, I. *Journal of the Faculty of Science, Hokkaido University*, Series VI, Zoology, 20, 230–243.
Kubota, S. (1979) Morphological notes on the polyp and medusa of *Climacocodon ikarii* Uchida (Hydrozoa, Margelopsidae) in Hokkaido. *Journal of the Faculty of Science, Hokkaido University*, Series VI, Zoology, 22, 122–136.
Kubota, S. (1993) Resting stage and newly hatched hydroid of a cool water hydrozoan species *Climacocodon ikarii* Uchida (Hydrozoa, Margelopsidae). *Publications of the Seto Marine Biological Laboratory*, 36, 85–87.
Kühn, A. (1913) Entwicklungsgeschichte und Verwandtschaftsbeziehungen der Hydrozoen. I. Teil: Die Hydroiden. *Ergebnisse und Fortschritte der Zoologie*, 4, 1–284.
Lesson, R.P. (1830) Voyage autour du monde, pendant les années 1822, 1823, 1824 et 1825. Zoologie. Description des zoophytes échinodermes. *Voyage de la Coquille II, II*, 20, 155 pp.
Lütken, C. (1850) Nogle Bemaerkninger om Medusernes systematiske Inddeling, navnlig med Hensyn til Forbes's History of Brittish naked-eyed medusae. *Videnskabelige Meddelelser fra den Naturhistoriske Forening i Kjöbenhavn*, 1850, 15–35.
Mayer, A.G. (1910) Medusae of the world. Volume I. The hydromedusae. *Carnegie Institution of Washington, Publication*, 109, 1–230.
McCrady, J. (1859) Gymnopthalmata of Charleston Harbor. *Proceedings of the Elliott Society of Natural History*, 1, 103–221.
Miner, R.W. (1950) *Field book of seashore life*. G.P. Putnam's Sons, New York, 888 pp.
Nawrocki, A.M., Collins, A.G., Hirano, Y.M., Schuchert, P. & Cartwright, P. (2013) Phylogenetic placement of *Hydra* and relationships within Aplanulata (Cnidaria: Hydrozoa). *Molecular Phylogenetics and Evolution*, 67, 60–71.
http://dx.doi.org/10.1016/j.ympev.2012.12.016
Owen, R. (1843) *Lectures on the comparative anatomy and physiology of the invertebrate animals: delivered at the Royal College of Surgeons, in 1843*. Longman, Brown, Green, & Longmans, London, 392 pp.
Petersen, K.W. (1979) Development of coloniality in Hydrozoa. *In*: Larwood, G. & Rosen, B.R. (Eds.), *Biology and systematics of colonial animals*. Academic Press, New York, pp. 105–139.
Petersen, K.W. (1990) Evolution and taxonomy in capitate hydroids and medusae (Cnidaria: Hydrozoa). *Zoological Journal of the Linnean Society*, 100, 101–231.
http://dx.doi.org/10.1111/j.1096-3642.1990.tb01862.x
Rees, W.J. (1941) Notes on British and Norwegian hydroids and medusae. *Journal of the Marine Biological Association of the United Kingdom*, 25, 129–141.
http://dx.doi.org/10.1017/S002531540001434X
Rees, W.J. (1957) Evolutionary trends in the classification of capitate hydroids and medusae. *Bulletin of the British Museum* (*Natural History*), *Zoology*, 4, 453–534.
Ritchie, J. (1915) The hydroids of the Indian Museum. II.–*Annulella gemmata*, a new and remarkable brackish-water hydroid. *Records of the Indian Museum*, 11, 541–568.
Sanders, A.E. & Anderson, W.D. Jr. (1999) *Natural history investigations in South Carolina from colonial times to the present*. University of South Carolina Press, Columbia, 333 pp.
Sandifer, P.A., Smith, T.I.J. & Calder, D.R. (1974) Hydrozoans as pests in closed-system culture of larval decapod crustaceans. *Aquaculture*, 4, 55–59.
Sandine, P.H. & Swiecicki, F.A. (1975) Zooplankton. *In: Ecological studies in the bays and other waterways near Little Egg Inlet and in the ocean in the vicinity of the proposed site for the Atlantic Generating Station, New Jersey. Vol. II.* Ichthyological Associates, Inc., Ithaca, New York, pp. 72–94.

Schuchert, P. (1996) The marine fauna of New Zealand: athecate hydroids and their medusae (Cnidaria: Hydrozoa). *New Zealand Oceanographic Institute Memoir*, 106, 1–159.
Schuchert, P. (2006) The European athecate hydroids and their medusae (Hydrozoa, Cnidaria): Capitata Part 1. *Revue Suisse de Zoologie*, 113, 325–410.
http://dx.doi.org/10.5962/bhl.part.80356
Stephens, L.D. (2000) *Science, race, and religion in the American South. John Bachman and the Charleston circle of naturalists, 1815–1895*. University of North Carolina Press, Chapel Hill, 338 pp.
Stephens, L.D. & Calder, D.R. (1992) John McCrady of South Carolina: pioneer student of North American Hydrozoa. *Archives of Natural History*, 19, 39–54.
http://dx.doi.org/10.3366/anh.1992.19.1.39
Tatham, T.R., Sandine, P.H., Smith, R.P., Hoffman, H.W., Tighe, K.A. & Thomas, D.L. (1977) *Ecological studies for the Oyster Creek Generating Station. Progress report for the period September 1975 – August 1976. Volume Two. Plankton.* Ichthyological Associates, Inc., Ithaca, New York, 368 pp.
Thiel, M.E. (1938) Die Leptolinae der „Meteor"-Expedition in systematischer Betrachtung. (I. Anthomedusae). *Zoologischer Anzeiger*, 121, 289–303.
Uchida, T. (1924) On a new "pelagic" hydroid, *Climacocodon ikarii* n. gen., n. sp. *Japanese Journal of Zoology*, 1, 59–65.
Uchida, T. (1927) Studies on Japanese hydromedusae. 1. Anthomedusae. *Journal of the Faculty of Science, Imperial University of Tokyo*, Section IV, Zoology, 1, 145–241.
Verrill, A.E. (1865) Classification of polyps: (extract condensed from a synopsis of the Polypi of the North Pacific Exploring Expedition, under Captains Ringgold and Rodgers, U.S.N.). *Proceedings of the Essex Institute*, 4, 145–152.
Werner, B. (1954) On the development and reproduction of the anthomedusan, *Margelopsis haeckeli* Hartlaub. *Transactions of the New York Academy of Sciences*, Series 2, 16 (3), 143–146.
http://dx.doi.org/10.1111/j.2164-0947.1954.tb02321.x
Werner, B. (1955a) On the development and reproduction of the anthomedusan *Margelopsis haeckeli* Hartlaub. *Annals of the New York Academy of Sciences*, 62, 1–30.
http://dx.doi.org/10.1111/j.1749-6632.1955.tb35352.x
Werner, B. (1955b) Über die Fortpflanzung der Anthomeduse *Margelopsis haeckeli* Hartlaub durch Subitan- und Dauereier und die Abhängigkeit ihrer Bildung von aüßeren Faktoren. *Verhandlungen der Deutschen Zoologischen Gesellschaft*, 1954, 124–133.
Werner, B. (1956) Der zytologische Nachweis der parthogenetischen Entwicklung bei der Anthomeduse *Margelopsis haeckeli* Hartlaub. *Naturwissenschaften*, 43 (23), 541–542.
http://dx.doi.org/10.1007/BF00629371
Zamponi, M.O. (1983) Nuevas adiciones a la medusofauna de la region Subantartica. I. Anthomedusae y Narcomedusae (Coelenterata: Hydrozoa). *Neotropica*, 29, 173–181.